NOTES ON THE DISTRIBUTION, HABITS, AND HABITATS OF SOME PANAMA CULICINES (DIPTERA: CULICIDÆ)

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(Continued from Vol. LVII, p. 233)

In the third part of this paper, I concluded the discussion of the habits, habitats, and distribution of the individual species of Panama mosquitoes. In this concluding part I am offering some general observations on the ecology of Panama mosquitoes.

PART IV

ECOLOGY

The Republic of Panama is that twisted, sigmoid-shaped ribbon of land lying between latitudes 8° and 10° north, which connects the American continents and separates the almost merging waters of the Atlantic and Pacific Oceans. The building of the canal disturbed such faunistic distinctions as the area might have had. Therefore, as much as it might be desired that the following discussion be limited to a natural faunistic area, for all practical purposes, the area under consideration lies within the present boundaries of the Republic of Panama, which extends from Costa Rica on the west to Colombia on the east, and from the Caribbean Sea on the north, to the Pacific Ocean on the south. The coast line is irregular longest on the Pacific side, some 674 miles, and about 379 miles on the Atlantic side. The isthmus is wider at the extremities, narrowing at the Canal Zone to about 35 miles. Spread over nearly all of its 32,000 square miles are mountains of varying heights, the highest about 11,000 feet located near the Costa Rican border. These gradually decrease on approaching the Canal Zone until they become a series of low hills ranging from fifty to several hundred feet in height. Then they again rise to higher elevations towards the Colombian border. There are, however, low stretches of land on the Pacific side extending in both directions from Panama City and forming natural grass plains. The drainage is primarily that of the Chagres river and its tributaries; however, numerous small rivers cut down between the hills and mountains draining into both oceans.

Considerable variation occurs in the climate in different parts of the Isthmus. In general, it is hot and humid with heavy rainfall. In the higher regions it is cooler, approaching temperate climates. In the Canal Zone, the days are hot, but the evenings are generally cool. The temperature varies between 70 and 85 degrees. Extremes of 60 to 100 degrees have occurred only on a few occasions. However, the constantly high relative humidity, which varies between 72% and 91% according to the location and season gives the feeling of great heat. The most extreme variation in the climate is that of rainfall. On the Pacific side of the continental divide the annual rainfall is 70 inches, while on the Atlantic side it is 130 inches or more. This leaves a marked effect on the vegetation, that of the Pacific side being much less rank than that of the Atlantic side.

From the middle of December to the first of May the trade winds blow from the north to the south, carrying away rain clouds, and thus contributing to the so-called "dry season." This period is characterized by clear cloudless skies and a constant breeze. It is then that the marked difference between the Atlantic side and the Pacific side is most noticeable. The vegetation on the Pacific side becomes parched and brown, while that of the Atlantic side remains green, for even during the dry season, the Atlantic side receives a fair amount of precipitation, while on the Pacific side it seldom rains. But during the other eight months of the year, known as the rainy season, the precipitation is much greater on both sides, reaching its height in November. This warm, humid climate favors the rapid growth of tropical vegetation and the abundance of water affords extensive areas suitable for the breeding of mosquitoes.

It is unfortunate that an extensive study of the fauna and flora of the Canal Zone was not made before the flooding of the Chagres valley, for even with what information we do have it is evident that considerable changes in the mosquito fauna have been wrought by the construction of the canal. Swamps have

FIG. 1. Washing clothes in a stream near Puerto de la Chorrera. This stream is a favorite breeding place of *Anopheles punctimacula* D. & K. in spite of the frequently soapy water.

FIG. 2. Rio Gatun, near Gatun Lake, showing the extent of "Najas" beds breeding *Anopheles albimanus* Wied. at the rate of 10 per dip.

Fig. 3. Dr. K. E. Frick collecting the larvæ of *Wyeomyia pseudopecten* D. & K. from the flower bracts of *Heliconia* sp.

Fig. 4. The main street of Puerto de la Chorrera, a typical small Panamian town. This town had a high malaria index. (See vol. LV, p. 195 for information on the breeding of *Anopheles albimanus* Wied. near this town.)

been drained and filled in. Concrete drains have been laid to conduct the surface water to large streams and lakes. Ponds and small lakes in some cases have been eliminated. In many areas, therefore, few mosquitoes can now be found where formerly many species were recorded. Moreover, as pointed out by Knab, nearly all of the bamboo formerly growing along the Chagres river has been destroyed, with hardly a clump remaining. Several species of mosquitoes inhabited that plant. Comparing recent records with Busck's records, it is evident that these species have disappeared from the Zone and must be found in other areas. There is even the possibility that some species have been exterminated. On the other hand, such species as inhabit or are associated with aquatic plants have greatly increased in number due to the great increase in areas inhabitable by these plants, i.e. Gatun Lake.

The two primary factors, temperature and rainfall, affect mosquito habits and habitats. Temperature fluctuation will of course accelerate or retard the length of time for the species to complete its life cycle. Rainfall fluctuation will in most cases regulate the area in which a species may breed. The following chart showing rainfall and temperature variation in Panama will give a key to the relative abundance of a given species of mosquito throughout the year. For instance, a species that breeds in temporary pools will be most abundant during the beginning of the rainy season. Later, during the heavy rains, the species may be less abundant due to "wash outs." Conversely, a species such as *Anopheles kompi* which is apparently restricted to drying, isolated pools in a stream bed, will be most abundant towards the end of the dry season. Leaf bract breeders such as species of *Wyeomyia* will show little variation in abundance throughout the year on the Atlantic side where the rainfall is sufficient the year around to keep water in the bracts. However, on the Pacific side where it is much dryer, leaf bract breeders will not be in evidence during the dry season. The effect of temperature is not so evident in Panama, there being a relatively slight fluctuation. However, the hot period at the end of the dry season on the Pacific side undoubtedly is a factor in the successful completion of the life cycle of such temporary pool breeders, as *Anopheles strodei* becomes during the dry season.

TEMPERATURE & RAINFALL 1934

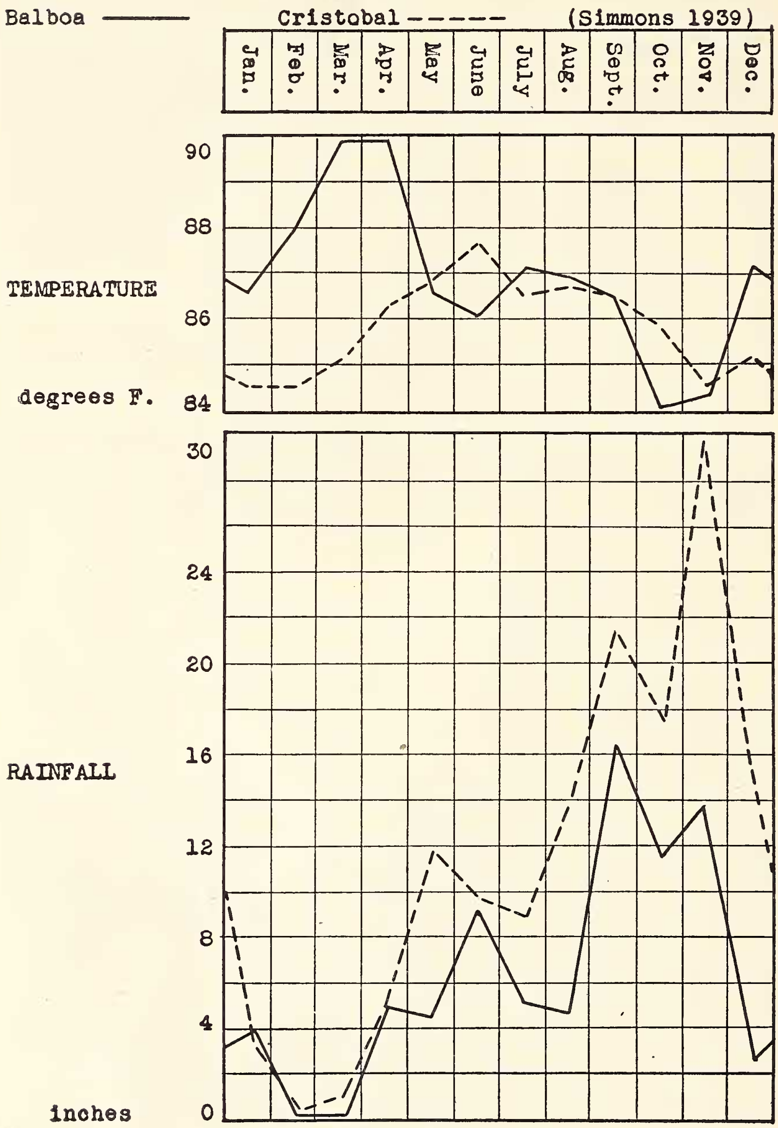

CHART I

Shannon (1931) restates a fundamental principle of mosquito biology, an original proposition of Howard, Dyar, and Knab, which is here quoted: "The larvæ of each species are more or less restricted to a special type of habitat; and further, the natural classification of the family as based on larval and adult characters is in accord with the natural classification of the habitats." He then goes on in his paper to show how this is true using as his example 86 Brazilian species. Further he shows how the larval habitats may be classed, based on location. The following study of 76 species of mosquito larvæ, from Panama follows Shannon's method and agrees with his work in all essential details.

Larval ecology. The striking differences between the larvæ of various habitats tempt one to undertake an elaborate ecological classification with or without special ecological terms, but one soon runs into difficulties. For example, it is difficult to draw precise limits between aerial habitats and surface habitats. It is also difficult to draw sharp distinctions on the basis of the nature of the habitats, since there are no precise limits between pools and lakes, or between swiftly running and more slowly moving water. This discussion is begun, therefore, with the following tabulation of the larval habitats.

LIST OF MOSQUITO LARVÆ OF PANAMA WITH THEIR PREFERRED HABITAT

Genus *CHAGASIA*

bathanus Dyar .... Shady, moderately swift streams.

Genus *ANOPHELES*

Subgenus *Stethomyia*

kompi Edwards .... Shady, drying pools or streams.

Subgenus *Anopheles*

eiseni Coquillett .... Rock holes, in shade.
pseudopunctipennis Theobald .... Sunny streams and pools with aquatic vegetation.
apicimacula Dyar & Knab .... Shady pools with debris.
neomaculipalpus Curry .... Sunny hoofprints or similar small ground pools.
punctimacula Dyar & Knab .... Sunny or shady surface water of many types.

Subgenus *Nyssorhynchus*

albimanus Wiedemann	Sunny lakes with aquatic vegetation.
albitarsis Arribalzaga	Sunny lakes usually with aquatic vegetation.
argyritarsis Robineau-Desvoidy	Sunny pools and streams.
strodei Root	Sunny or shady pools.
aquasalis Curry	Salty or fresh water ponds.
triannulatus Neiva & Pinto	Sun or shade, pools or lakes.

Subgenus *Kerteszia*

neivai Howard, Dyar & Knab	Bromeliads.

Genus *URANOTÆNIA*

calosomata Dyar & Knab	Shady, moderately flowing streams.
coatzacoalcos Dyar & Knab	Shady rock pools and streams.
geometrica Lutz	Small sunny pools with vegetation.
lowii Theobald	Small sunny pools with vegetation.
pulcherrima Lynch Arribalzaga	Floating river vegetation in sun.

Genus *MEGARHINUS*

hypoptes Knab	Tree holes.
moctezuma Dyar & Knab	Tree holes.
superbus Dyar & Knab	Leaf bracts of wild pineapple.

Genus *CULEX*

chidesteri Dyar	Open sunny swamps.
corniger Theobald	Usually clear shady small temporary pools.
coronator Dyar & Knab	Shady or sunny pools.
declarator Dyar & Knab	Shady or sunny surface pools or above surface containers.
quinquefasciatus Say	Artificial containers or foul pools.
inflictus Theobald	Crab holes.
interrogator Dyar & Knab	Sunny foul pools.
mollis Dyar & Knab	Shady rock holes.
nigripalpus Theobald	Sunny or shady foul pools.

Subgenus *Melanoconion*

aikeni Aiken	Floating river vegetation in sun.
bastigarius Dyar & Knab	Sunny streams with vegetation.
chrysonotum Dyar & Knab	Sunny, grassy pools.
conspirator Dyar & Knab	Shady rock pools.
dunni Dyar	Sunny swamps with grass.
eastor Dyar	Sunny foul pools.
educator Dyar & Knab	Sunny pools and streams with grass.
egcymon Dyar	Shady streams, no vegetation.
elevator Dyar & Knab	Shady rock holes.
erraticus Dyar & Knab	Ground pools and sluggish rivers.

Subgenus *Isostomyia*

conservator Dyar & Knab .... Tree holes.

Subgenus *Mochlostyrax*

hesitator Dyar & Knab .... Sunny pools with grass.
pilosus Dyar & Knab .... Sun or shade, salt or fresh water, permanent.

Subgenus *Lutzia*

allostigma Howard, Dyar & Knab... Rock holes.

Genus *DEINOCERITES*

cancer Theobald .... Crab holes.
pseudes Dyar & Knab .... Crab holes.

Genus *MANSONIA*

titillans Walker .... Attached to *Pistia.*

Genus *ÆDEOMYIA*

squamipennis L. Arrib. .... Associated with but not attached to *Pistia.*

Genus *ORTHOPODOMYIA*

fascipes Coq. .... Tree holes and sewage.

Genus *ÆDES*

Subgenus *Stegomyia*

ægypti Linn. .... Artificial containers.

Subgenus *Finlaya*

terrens Walker .... Tree holes.

Subgenus *Ochlerotatus*

angustivittatus Dyar & Knab .... Shady temporary pools.
serratus Theobald .... Shady temporary pools.
tæniorhynchus Wiedemann .... Salt marshes.

Genus *HÆMOGOGUS*

argyromeris Dyar & Ludlow .... Bamboo joints, tin cans, and tree holes.
chalcospilans Dyar .... Coconut shells.
lucifer Howard, Dyar & Knab .... Bamboo joints, tin cans, and tree holes.

Genus *PSOROPHORA*

lineata Humboldt .... Sunny, grassy pond, temporary.

Subgenus *Janthinosoma*

ferox Humboldt .... Shady pools, clear, temporary.

Subgenus *Grabhamia*

confinnis L. Arrib. .... Temporary pools.

Genus *TRICOPROSOPON*

digitatum Rond. .... Coconut shells, tin cans, and bamboo.
compressum Lutz .... Coconut shells.

Subgenus *Hyloconops*

longipes Fab. .... Leaves of "Skunk Cabbage."

Genus *WYEOMYIA*

scotinomus Dyar & Knab .... Bromeliads.
celanocephala Dyar & Knab .... Bromeliads.
quasiluteoventralis Theobald .... Bromeliads.
arthrostigma Lutz .... Bamboo and tin cans.

Subgenus *Dendromyia*

personata Lutz .... Tree holes, bamboo, tin cans and coconut shells.
pseudopecten Dyar & Knab .... Leaves and flower bracts of Heliconia.
ulocoma Theobald .... Flower bracts of Heliconia.
complosa Dyar .... Leaves of "Skunk Cabbage."

Genus *LIMATUS*

durhami Theobald .... Bamboo, tin cans and coconut shells.
asulleptus Theobald .... Artificial containers.

Genus *SABETHES*

cyaneus Fab. .... Tree holes.

Subgenus *Sabethinus*

undosus Coq. .... Bamboo.

From this list it may be seen that certain general statements may be made regarding the habitat *preferences* of mosquito larvæ. However, a few words of explanation as to the basis of these statements are necessary. As will be seen from the detailed listing under each species, there are a number of radical exceptions for a good number of species. These exceptions are treated in two ways in the literature. The first way is to list the exceptions as something new and interesting. The fault here lies in the reader's interpretation of such data. The tendency seems to be to attach a great amount of importance to these exceptions giving them undue emphasis. The second way is to omit the exceptions, to totally disregard and attach no importance whatsoever to them, considering these records to be some kind of mistake of nature which should be overlooked. The fault here is obvious. There certainly is some importance in the matter even if trivial, and the minutæ should not be entirely disregarded. In this discussion, the "middle road" has been followed. The exceptions are all listed under each species, but only the preferred habitat is considered; the preferred habitat as defined here is that habitat in which the great majority of individuals were found. Now that also has a serious disadvantage which is well illustrated by an example furnished in a collection of *Orthopodomyia fascipes.* In the course of the authors collecting, a great number of tree holes, the usual habitat of this species, was examined. A very few individuals were collected and this species is considered to be uncommon in the zone. However, one collection was made which yielded literally tens of thousands of larvæ. That was in a cement cess pool type latrine which held the sewage for natural digestion with an effluent into a nearby river. Obviously the habitat was well suited for the breeding of this species, yet it can hardly be called the "preferred" habitat. Still, it cannot be disregarded. The advantage of using the "preferred habitat" becomes apparent when one attempts to correlate the habitats of the species with the classification of the species based on morphology.

For convenience in discussion, the habitats of the larvæ are here divided into three groups. (1) Surface habitats, which include all water either of a permanent or a temporary nature which are impressions in the earth, such as lakes, pools, streams, swamps, rock holes, rain pools, whether or not they are man made, e.g. dams, borrow pits, etc., or animal made, e.g. hoofprints, crab holes, etc. Under this division have been included crab holes, but because of the specialized nature of the habitat they are considered separately instead of with the stagnant pools. The mosquitoes of this habitat have undergone distinct morphological changes which have enabled them to maintain a successful existence. (2) Aerial (above surface) habitats, which include all natural collections of water above the surface and in all cases surrounded by plant tissue. This includes hollow logs, stumps, tree holes and leaf and flower bracts of plants. (3) Artificial containers which include man made habitats such as tin cans, pots, dishes, machinery, etc. This habitat is distinct only in that it has existed in recent times. The mosquitoes breeding in such habitats certainly must, under normal conditions, breed in one or both of the other two types of habitats, and many species still do.

From the "preferred" habitat list then, we can make the following classification of the mosquitoes of Panama based on the larval habitats according to position.

I. Surface water
  A. Flowing
    1. Shady
      Chagasia bathanus; Anopheles punctimacula; Uranotænia calosomata, U. coatzacoalcos; Culex egcymon.
    2. Sunny
      Anopheles pseudopunctipennis, A. punctimacula, A. argyritarsis; Uranotænia pulcherrima; Culex aikeni, C. bastigarius, C. erraticus; Mansonia titillans; Aedeomyia squamipennis.
  B. Stagnant (Permanent)
    1. Shady
      Anopheles kompi, A. eiseni, A. apicimacula, A. strodei, A. triannulatus; Uranotænia coatzocoalcos; Culex coronator, C. declarator, C. mollis, C. nigripalpus, C. conspirator, C. elevator, C. pilosus, C. allostigma.
    2. Sunny
      Anopheles pseudopunctipennis, A. neomaculipalpus, A. punctimacula, A. albimanus, A. albitarsis, A. argyritarsis, A. strodei, A. aquasalis, A. triannulatus; Uranotænia geometrica, U. lowii; C. chidesteri, C. coronator, C. declarator, C. quinquefasciatus, C. interrogator, C. nigripalpus, C. chrysonotum, C. dunni, C. eastor, C. educator, C. hesitator, C. pilosus, C. allostigma; Aedes tæniorhychus.
  C. Stagnant (Temporary)*
      Anopheles neomaculipalpus; Culex corniger; Aedes angustivittatus, A. serratus; Psorophora lineata, P. ferox, P. confinnis.
  D. Crab holes.
      Culex inflictus; Deinocerites pseudes.
II. Aerial habitats

* Many species will breed in temporary bodies of water. This list includes only those especially addicted to temporary water collections.

A. Close to or on the ground (Buttress roots, bamboo sections, coconut shells, palm spathes, etc.)
Culex declarator; Hæmagogus argyromeris, H. chalcospilans, H. lucifer; Trichoprosopon digitatum, T. compressum; Wyeomyia arthrostigma, W. personata; Limatus durhami; Sabethes undosus.

B. Leaf and flower bracts of terrestrial plants.
Megarhinus superbus; Trichoprosopon longipes; Wyeomyia pseudopecten, W. ulocoma, W. chalcocephala, W. complosa.

C. Tree holes
Megarhinus hypoptes, M. moctezuma; Culex conservator; Orthopodomya fascipes; Aedes terrens; Hæmagogus argyromeris, H. lucifer, Wyeomyia personata; Sabethes cyaneus.

D. Epiphytic Bromeliads
Anopheles neivai; Wyeomyia melanopus, W. scotinomus, W. celanocephala, W. quasiluteoventralis.

III. Artificial containers
Culex quinquefasciatus; Orthopodomyia fascipes; Aedes ægypti; Hæmogogus argyromeris, H. lucifer; Trichoprosopon digitatum; Wyeomyia arthrostigma, W. personata; Limatus durhami, L. asulleptus.

Thus far only the position of the habitat has been considered. Further division of these habitats could be made by taking into account the type of water in the receptacles. For example, the salt content. Some species are known to be especially addicted to salt water. Of these, *Anopheles aquasalis, Culex pilosus* and *Aedes tæniorhynchus* are the Panama species collected in salt water. The first are commonly found in fresh as well as salt water. The last species is a well known salt marsh breeder and is seldom collected elsewhere. Another example of habitat division could take into account whether the water is foul, clear, or turbid, etc. However, it is the author's opinion that a great deal more observation and experimentation are necessary before any conclusions can be drawn regarding the role of these factors in the habitats of these mosquitoes.

Plant associations: The association of aquatic plants with mosquitoes is a fairly well known phenomenon. There is a considerable amount of literature on the subject, some dealing with the aquatic plant as a nursery for the immature stages and some as an inhibitor of mosquito breeding. There are three striking aquatic plant associations in Panama. The first is the breeding of *Anopheles albimanus* in extensive floating beds of *Najas.* These floating Najas beds are to be found in the Chagres and Gatun rivers and in Gatun Lake, especially during the dry season. These beds extend for miles in the quiet waters of these rivers and lakes. The high water during the rainy season breaks these beds and they sink below the surface. But during the dry season *albimanus* breeds in great numbers protected by the protruding leaves. Another association is that between *Mansonia titillans* and *Pistia stratiotes* Linn. The larvæ of *titillans* attach themselves almost exclusively to the roots of this plant. *Anopheles triannulatus* breeding in rivers is found nearly always inside the partly submerged rosettes of leaves of *Pistia. Aedeomyia squamipennis* is found closely associated with the roots of *Pistia,* but not attached to them as are the larvæ of *titillans.*

Predaceous larvæ: Some of the mosquito larvæ have ceased to be vegetable and small animal feeders and have developed a more active means of feeding. There are ten Panama species which we reared or observed feeding on other mosquito larvæ. Of these, some have the mouth-brushes modified for seizing prey and others have the mandibles and maxillæ modified. Three tribes are represented, the Megarhinini, the Culicini and the Sabethini. Of the first two mentioned, the hairs of the mouth-brushes are strong and rod-shaped, used for grasping other larvæ. The Sabethini do not have adapted mouth-brushes but rather the mandibles and maxillæ are changed to facilitate predaceous activities.

These predaceous mosquito larvæ are as follows: *Megarhinus hypoptes,* feeding on *Hæmogogus argyromeris, H. lucifer, Wyeomyia personata, W. arthrostigma; Megarhinus moctezuma* feeding on *Culex conservator, Hæmogogus argyromeris; Megarhinus superbus* feeding on *Wyeomyia scotinomus, W. quasiluteoventralis; Culex allostigma* feeding on *Chagasia bathanus, Anoph-*

eles kompi, A. eiseni, A. apicimacula, A. punctimacula, A. argyritarsis, A. strodei, Uranotænia coalzacoalcos, Culex coronator, C. corniger, C. declarator, C. mollis, C. conspirator, Hæmagogus argyromeris, H. lucifer; Psorophora lineata feeding on *Trichoprosopon digitatum; Trichoprosopon digitatum* is cannibalistic; *Trichoprosopon compressum* feeding on *Wyeomyia personata; Trichoprosopon longipes* feeding on *Wyeomyia pseudopecten, W. complosa; Sabethes cyaneus* and *Sabethes undosus* feeding on *Aedes ægypti* (in the laboratory).

From this list, it is observed that there is apparently little preference as to the food of these larvæ. They seem quite willing to eat any larvæ that happen to be in the same habitat with it, and as far as is known, none of the prey have developed modifications to protect themselves from their destroyers. However, some of the predaceous larvæ have developed moderately long and stout body hairs which undoubtedly prevent cannibalism. An example of this is the larva of *Sabethes undosus.*

Unfortunately there are no records from Panama as to other organisms which are eaten by these larvæ. Further observation is necessary to determine whether these larvæ are partial to other mosquito larvæ because of their characteristic motion, or whether they will readily eat any conveniently sized organism whose motion attracts their attention. In the laboratory, however, nine of the ten species listed were reared. Each of these species readily ate the larvæ of colony reared *Aedes ægypti.*

Adult ecology: The great change from an aquatic existence to a terrestrial mode of life, of course, greatly complicates the habits of any organism. This holds true for mosquitoes. Aside from the obvious morphological changes which take place, there are as great changes in the physiology. A new source of food has to be acquired and new habits developed in this new habitat.

Unfortunately, very little is known about adult mosquito habits as compared with larval habits. We are well aware of the fact that mosquitoes will make use of mammal blood. In addition, among the Sabethines a few species have been reported as feeding on reptile blood. But we do not know what their other feeding habits may be. What role does plant food play in the lives of these organisms? Do they have food preferences? If so, what effect does this have on the breeding habits of the larvæ? Does the female lay her eggs near her plant food?

Species known to bite man: Finally, there is one factor in adult ecology which has received attention. That is the human feeding habits of mosquitoes. The following species of the Panama fauna are known to bite man:

Anopheles pseudopunctipennis, A. apicimacula, A. neomaculipalpus, A. punctimacula, A. albimanus, A. neivai, Culex quinquefasciatus, C. nigripalpus, C. inflictus, deinocerites pseudes? (in houses), *Mansonia titillans, M. arribalzagæ, M. nigricans, M. fasciolatus, Aedeomyia squamipennis?* (in human bait traps), *Aedes ægypti, A. quadrivittatus, A. terrens, A. fulvus, A. serratus, A. tæniorhynchus, Hæmagogus argyromeris, H. lucifer, H. equinus, Psorophora lineata, P. ferox, P. lutzi, P. confinnis, P. cyanescens, Trichoprosopon digitatum, T. compressum, T. espini, Wyeomyia celanocephala, W. personata, W. melanocephala, Limatus durhami, Sabethes cyaneus, S. chloropterus, S. undosus.*

The preceding list contains only those species which have been observed actually to bite, with the exceptions so marked and explained in the following parentheses.

There are many other species which will and do no doubt feed on human blood. Many other species have been collected in horse traps which undoubtedly will feed on humans, but they are not listed because they have never actually been observed to bite man.

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